Shyer and larger bird species show more reduced fear of humans when living in urban environments

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ABSTRACT

As the natural habitats of many species are degraded or disappear, there is scope for these species to be established in urban habitats. To ease the establishment and maintenance of urban populations of more species we need to better understand what degree of phenotypical change to expect as different species transition into urban environments. During the first stages of urban colonisation, behavioural changes such as an increase in boldness are particularly important. A consistent response in urban populations is to decrease the distance at which individuals flee from an approaching human (flight initiation distance, or FID). Performing a Phylogenetic Generalised Least Squares (PGLS) analysis on 130 avian species, I found that the largest changes in FID between rural and urban populations occur in species that are larger-bodied and naturally shy (higher rural FID), two phenotypic traits that are not normally associated with urban colonisers. More unlikely species may thus be able to colonise urban environments, especially if we design cities in ways that promote such urban colonisations.

Keywords: birds; body mass; FID; flight initiation distance; urban ecology; urbanisation

INTRODUCTION

The colonisation of urban environments by animals requires behavioural adjustments that maximise their fitness in these novel environments [1]. In particular, urban animals may benefit by decreasing their fear towards humans and other anthropogenic stimuli [2], as repeatedly fleeing from approaching humans and vehicles is energetically costly and prevents animals from optimal foraging and other relevant activities [3]. A well-supported measure of increased boldness in urban animals is shorter flight initiation distances (FID, methodologically defined as the distance at which an individual flees when approached by a human) [4-7]. There is inter-individual variability in FID within a species, although individuals within a population typically display consistent FIDs over time [8-10]. Importantly, in both intraspecific and interspecific studies, urban populations consistently have shorter FIDs than their rural counterparts [5-8, 11-13].

The differences in FID observed between urban and rural populations may arise from behavioural plasticity or adaptation after a species colonises an urban environment [14-16]. Species that are naturally bolder (i.e. with relatively small rural FID) may be more likely to initiate such urban colonisations [17; however, see 7]. Assuming similar selective pressures in the same urban environment across species, these naturally bolder species may not need to decrease their FIDs to the same degree as species that colonise the same urban environments but are naturally shyer (i.e. those with a relatively larger rural FID) [18]. That is, naturally shyer species may undergo greater behavioural changes when transitioning from rural to urban environments. Alternatively, urban colonisation may be restricted to only the boldest individuals, resulting in an immediate differentiation in FID between urban and rural populations [7]. Under this scenario, the initial change in FID between rural and urban populations may be similar across species independently of whether these species are naturally bold or shy. However, after urban establishment, those species that are naturally shy may need to further decrease their FIDs via phenotypical plasticity or adaptation in order to succeed under urban conditions. This will also result in naturally shyer species being the ones changing the most when completing their transition from rural to urban environments.

I thus hypothesised that naturally shy species (high rural FID) will experience a higher degree of behavioural change in order to successfully colonise urban environments. Here, I addressed this hypothesis by quantifying the change in FID (ΔFID) between rural and urban populations in 130 avian species and determining how this change is associated with natural shyness. I also considered the effect of body mass, as FID is consistently higher in larger species [4, 5, 11, 19]. A positive association between ΔFID and rural FID would indicate that naturally shy species need to change the most when colonising urban environments, thus supporting the above hypothesis. No association would indicate that all species change similarly in response to urbanisation, regardless of their rural FID. Finally, a negative association would indicate that naturally shy species remain relatively shy under urban conditions, possibly by only invading urban areas with low levels of disturbance where they can maintain long FIDs that are still compatible with normal levels of activity.

METHODS

I made bibliographical searches in Web of Science up to 6 July 2017, using the term "urban*" combined with one of the following terms: "flight initiation distance", "flight distance", "escape distance", "flushing distance", "flush distance", or "disturbance distance". I compiled information from avian species on FID when this was available for both urban and rural populations. I only considered species in which both FID values were calculated using measurements from more than one individual. When values for the same species were available from more than one source, I used the study with larger sample sizes. I also obtained body mass for each species. The compiled dataset (see supplementary material) consisted of information from 130 species.

I conducted a phylogenetic generalised least-squares (PGLS) analysis in R (v.3.4.1) using the caper v0.5.2 package [20]. A PGLS includes the phylogenetic structure of the species under consideration as a covariance matrix within a linear model. An estimated phylogenetic scaling parameter lambda (λ) takes values from 0 to 1, with values close to 0 indicating that the relationship between the variables is largely independent of phylogeny, and values close to 1 indicating a strong association with phylogeny. For the phylogenetic reconstruction, I combined information from several sources, using Mesquite v.3.2 (see supplementary material for such sources and the resulting phylogeny). All variables were $\log_{10}$ transformed prior to analysis. A PGLS model included the relative change in FID as the response variable (ΔFID / rural FID), and body mass and rural FID (or natural level of shyness) as factors. An additional PGLS included the absolute ΔFID between rural and urban populations as the response variable.

RESULTS

As expected, across species rural FID was higher (mean ± SD: 22.18 ± 22.04 m; range: 4.93 – 180 m) than urban FID (mean ± SD: 8.60 ± 5.29 m; range: 2.31 – 33.50 m; paired t-test: $t_{129} = -15.49$, $p < 0.0001$). Accordingly, rural FID was higher than urban FID in most species, although there were a few exceptions (absolute ΔFID mean ± SD: 13.63 ± 20.29 m; range: -11.78 – 167.58 m). Implementing a sequential sums of squares PGLS ($\lambda = 0.17$), I found a positive association between body mass and relative ΔFID between rural and urban populations ($F_{1,127} = 8.18$, $p = 0.005$). After removing the effect of body mass, a positive association was also apparent between natural shyness and relative ΔFID between rural and urban populations ($F_{1,127} = 7.37$, $p = 0.008$; Fig. 1). The positive association between natural shyness and ΔFID was also strong even without including body mass in the model ($\lambda = 0.17$; $F_{1,128} = 15.60$, $p = 0.0001$). Natural shyness was also positively associated with an absolute change in FID ($\lambda = 0.32$; $F_{1,127} = 41.05$, $p < 0.0001$; body mass was also included in this model: $F_{1,127} = 32.24$, $p < 0.0001$).

Results were qualitatively similar when considering only those species for which sample sizes for both urban and rural FIDs were ≥ 5 (N = 103; $\lambda = 0.50$; positive association between natural shyness and relative ΔFID between rural and urban populations: $F_{1,100} = 6.56$, $p = 0.01$; body mass also had a significant effect on relative ΔFID: $F_{1,100} = 5.47$, $p = 0.02$).

DISCUSSION

I found that species that are naturally shyer are the ones that experience a higher change in FID when colonising urban environments. The mechanism underlying this association remains unclear. If changes in FID occur in response to the new conditions experienced by individuals in urban environments, such changes have to be driven by local adaptation or phenotypic plasticity [15], and any of these processes would be more intensely acting on individuals from naturally shyer species. Alternatively, if bolder individuals in the rural populations are the ones driving urban colonisations [7, 13], the results of this study suggest that those species that are in average shyer (i.e. with higher average rural FID) are also the ones with higher variation in FID [21]. If this is true, further investigation is required to elucidate how this large variation is maintained in species with high average rural FID, e.g. different behavioural strategies may exploit different social and/or environmental conditions. All the above processes are obviously non-exclusive, and there may be species in which the boldest individuals within a species are the ones colonising urban environments, then FID within the resulting urban population becomes shorter through behavioural plasticity, and it may be even further decreased through adaptation depending on selective pressures.

I also found that larger species experience a higher change in FID when making the transition from rural to urban environments, echoing results found in a recent meta-analysis [21]. Large species in urban environments may suffer less predation than small-sized species, and this reduced predation risk may lead to an increased tolerance of humans [21, 22].

There are other factors here not considered that can also affect the difference in FID between urban and rural populations within a species. For example, the difference in FID between rural and urban populations may increase with the time since urbanization [5], as the more generations are raised under urban conditions the more opportunities for adaptations to urbanisation to occur, including increased boldness and thus reduced FID; however, see [23].

The fact that the higher change in FID between rural and urban populations occurred in species that are naturally shy and in larger species, two features that are not typical in successful urban colonisers, suggests that many more species than those currently described may have the potential to establish and maintain viable populations in urban environments, even those species that do not meet the characteristics normally associated with urban species. There is great scope to design urban environments that can promote the establishment of more species and their adaptation to these novel environments, for example by creating spaces where the close proximity to people and vehicle traffic is avoided [24, 25].

COMPETING INTERESTS

I have no competing interests.

DATA ACCESSIBILITY

All data used in the analyses are included as supplementary material.

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FIGURE CAPTIONS

Figure 1. The relative reduction of FID in urban populations is higher in those species that are naturally shyer after controlling for the effects of body mass and phylogenetic relationships. The log-transformed values for rural FID are shown in

the x axis, whereas the log-transformed relative change in FID (i.e. ΔFID divided by rural FID) are shown in the y axis. Values of shyness in rural populations are the residuals from a PGLS in which rural FID was the dependent variable and body mass was the independent variable ($F_{1,128} = 111$, $p < 0.0001$). Values of relative reduction of FID in urban environments are the residuals from a different PGLS in which relative ΔFID ((rural FID – urban FID) / rural FID) was the dependent variable and body mass was the independent variable ($F_{1,128} = 7.82$, $p = 0.006$). That is, the shown association accounts for both body mass and the effect of phylogeny. The same value of lambda ($\lambda = 0.17$) was used in both PGLS (a similar figure was obtained using maximum likelihood to calculate λ for each PGLS). Such an approach was used only to create this plot and not for the formal analysis.